

LARVAL DEVELOPMENT OF *PAGURUS ANNULIPES* (STIMPSON, 1862) AND *PAGURUS POLLICARIS* SAY, 1817
REARED IN THE LABORATORY

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The hermit crabs *Pagurus annulipes* (Stimpson, 1862) and *P. pollicaris* Say, 1817 are common hermits found in shallow subtidal water from Massachusetts south to Florida. The southern distribution of *P. annulipes* reaches some distance north of Miami on the east coast of Florida and on the west coast of Florida extends from perhaps central or northwestern Florida westward along the perimeter of the Gulf of Mexico at least to Texas (Provenzano, 1959 and personal communication; Rouse, 1969). *P. pollicaris*, perhaps a subspecies, is also found along the northern perimeter of the Gulf of Mexico from western Florida to Texas (Provenzano, 1959). In the Woods Hole, Massachusetts region these two species and *P. longicarpus* Say comprise the shallow-water hermit crab fauna.

The ovigerous season of *P. annulipes* extends from about May to the end of September and completely overlaps that of *P. longicarpus*. The season of *P. pollicaris* is from early spring to the end of June. These seasons have been determined by examination of adults and of limited plankton samples during the summers of 1967 and 1968.

A review of the literature on larvae of members of the genus *Pagurus* has been given by Coffin (1960). All recent literature is cited by Roberts (1970) with the exception of Forss and Coffin, 1960; Kurata, 1964 and 1968; and Greenwood, 1966.

This paper deals with the external anatomy of *P. annulipes* and *P. pollicaris* larvae. Utilizing the recent description of *P. longicarpus* larvae (Roberts, 1970), two keys to the larvae of the shallow-water hermit crabs found in the Woods Hole, Massachusetts region are given, one based on larval pigmentation and the other on larval external anatomy. Comparisons are made with other species of the genus *Pagurus* in the context of examining current views on groups within the genus.

MATERIALS AND METHODS

Ovigerous females were obtained from the Marine Biological Laboratory Supply Department of Woods Hole, Massachusetts during the summers of 1967 (*P. annulipes*) and 1968 (*P. pollicaris*). They were maintained in beakers until the eggs hatched. Larvae were transferred with a large bore pipette to small beakers and reared individually (*P. annulipes*) or in groups of 5 (*P. pollicaris*). Larvae were maintained at room temperature ($24 \pm 2^\circ \text{C}$) and at $16 \pm 0.5^\circ \text{C}$ (some *P. pollicaris*) in a controlled environment chamber with constant light. Water was changed and *Artemia* nauplii added as the culturing

conditions dictated, usually daily or every other day. Larvae were examined daily to determine duration of each stage. Because no *P. pollicaris* successfully molted to the megalopa, duration for the fourth zoeal stage, was determined by assuming a successful molt. In addition to laboratory-reared specimens the verbal description of *P. annulipes* larvae utilized specimens obtained from the plankton collected just off the Bureau of Commercial Fisheries Laboratory, Woods Hole, Massachusetts.

Both fresh and preserved (70% ethanol) larvae were dissected with micro-needles under the dissecting microscope. Details were checked using darkfield illumination. Verbal descriptions were based on 3 to 10 specimens except for carapace and total length. Depending on the stage, 4–108 specimens of *P. annulipes* (all planktonic) and 1 specimen of *P. pollicaris* were measured to determine lengths. Megalopal appendages of *P. pollicaris* were dissected out from incomplete molts, somewhat distorted and not fully expanded but adequate for description. Drawings were done from single specimens, using a camera lucida to give overall proportions with detail filled in by eye. Chromatophore patterns were determined from living larvae and larvae freshly killed in glycerine.

Throughout the descriptions the terminology of Roberts (1970) has been followed and the following abbreviations have been used: A1—antennule, A2—antenna, Mn—mandible, Mx 1—maxillule, Mx 2—maxilla, Mxp 1 to 3—first to third maxilliped, P 1 to 5—first to fifth pereopod, Pl 2 to 5—second to fifth pleopod, U—uropod. The verbal descriptions have been abridged to report only variations of a given character among specimens, *i.e.*, information not illustrated in the figures.

RESULTS

As in other species of the genus, *Pagurus annulipes* and *P. pollicaris* have 4 zoeal stages and a megalopa. No variation in the number of stages was observed and no living prezoecae were observed.

Pagurus annulipes (see Figs. 1–4): *Zoea I*

Duration 5.4 days ($N = 21$).

Carapace length 0.9–1.3 mm, av. 1.1 mm ($N = 108$).

Total length 1.9–2.4 mm, av. 2.2 ($N = 108$).

Carapace without processes except for posterolateral spines. Rostrum unornamented, long, drawn out to a thin point, curved slightly ventrally, slightly longer than the antennae, which are longer than the antennules. Eyes sessile. Six abdominal segments, the sixth fused to the telson. Segments 2 through 5 with 2 pairs of posterodorsal and 1 pair of ventrolateral small spines, the ventrolateral spines of segment 5 only slightly longer than the others. Pleopod buds and uropods absent.

Red chromatophores predominate. One complex present around mouthparts extending from the base of the antennules posteriorly on each side of the labrum to the base of the mandibles. A single large red chromatophore on midlateral portion of each side of carapace; a large red chromatophore in abdominal segments 2 and 3; and a complex in segments 5 and 6—telson. One small medial yellow

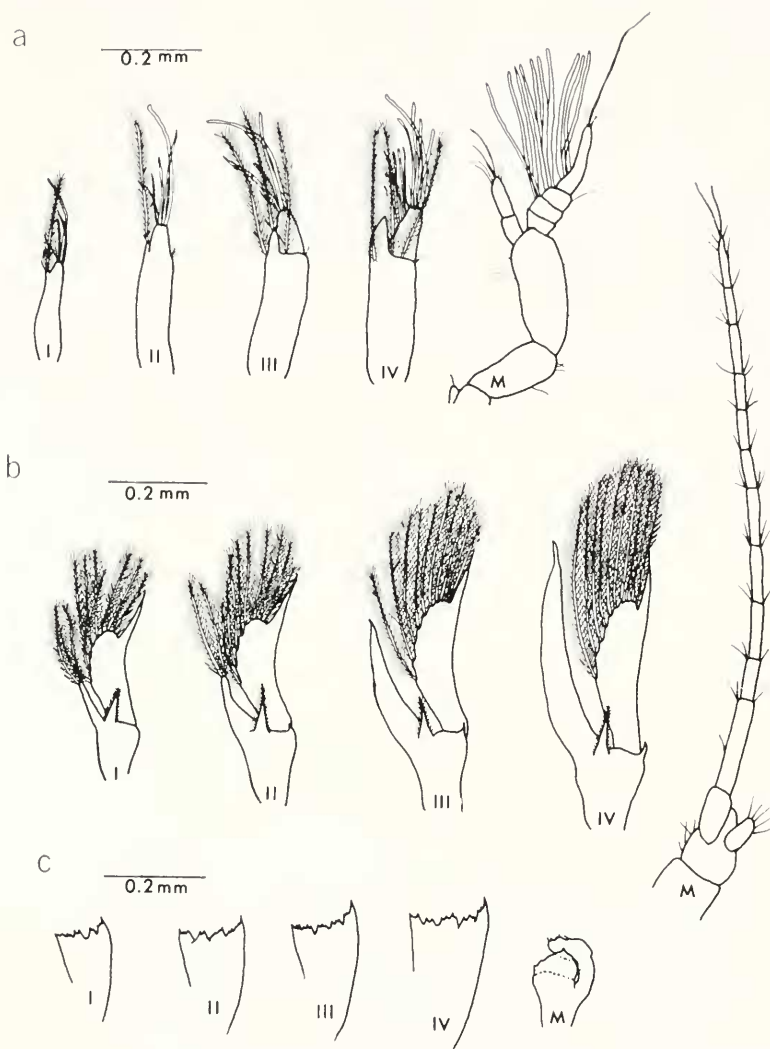


FIGURE 1. *Pagurus annulipes*; a. antennules, b. antennae, c. mandibles of zoeal stages I-IV and megalopa.

chromatophore in abdominal segment 6-telson. One large bar-shaped yellow chromatophore in cardiac region of thorax. Diffuse yellow pigment over dark pigment of eye.

A 1—With 1 long, 2 medium and 1 to 3 short terminal aesthetascs (A 1 similar in zoea II).

A 2—Scale with 8 plumose setae, 1 or 2 small setae medially.

Mx 1—Basal endite produced into 2 strong spines with 1 to 3 cuneate spinules each.

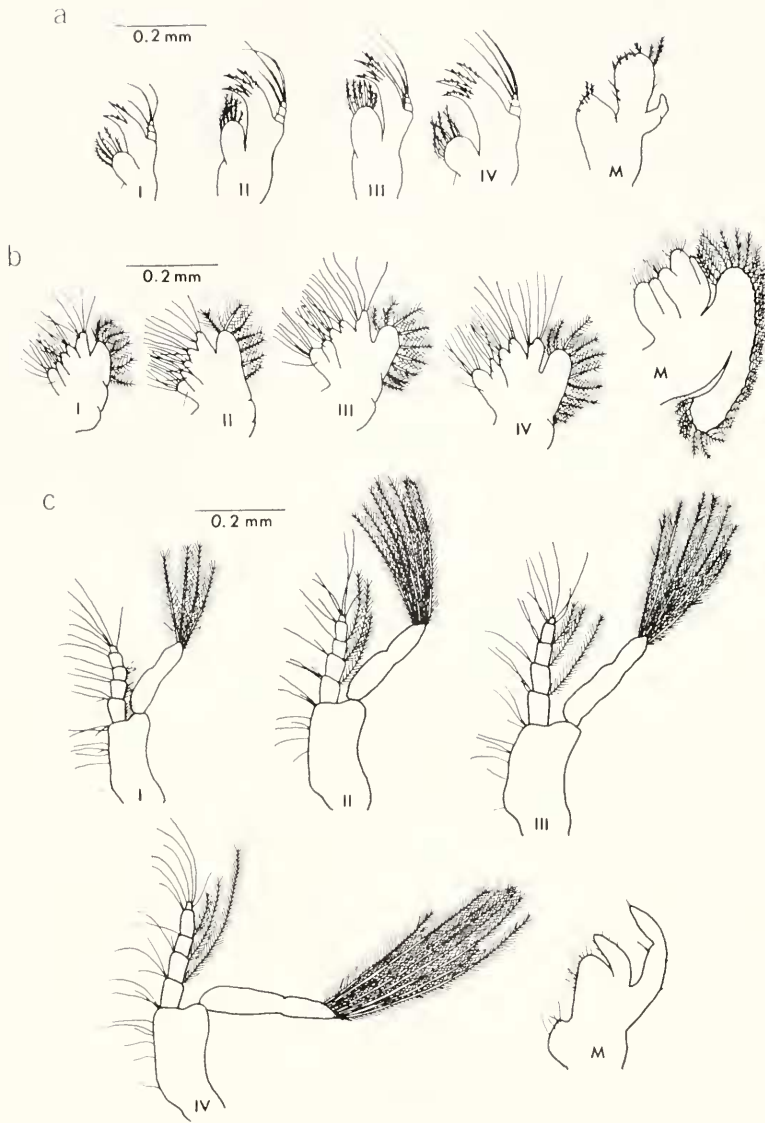


FIGURE 2. *Pagurus annulipes*; a. maxillules, b. maxillae, c. first maxillipeds of zoeal stages I-IV and megalopa.

Mx 2—Distal lobe of coxal endite with 3 or 4 terminal setae (similar in zoea II, III, IV). Endopod unsegmented with 2 or 3 subterminal setae.

Mxp 1—Basis with 5 to 6 long and 2 or 3 short medial setae (similar in zoea II, III, IV).

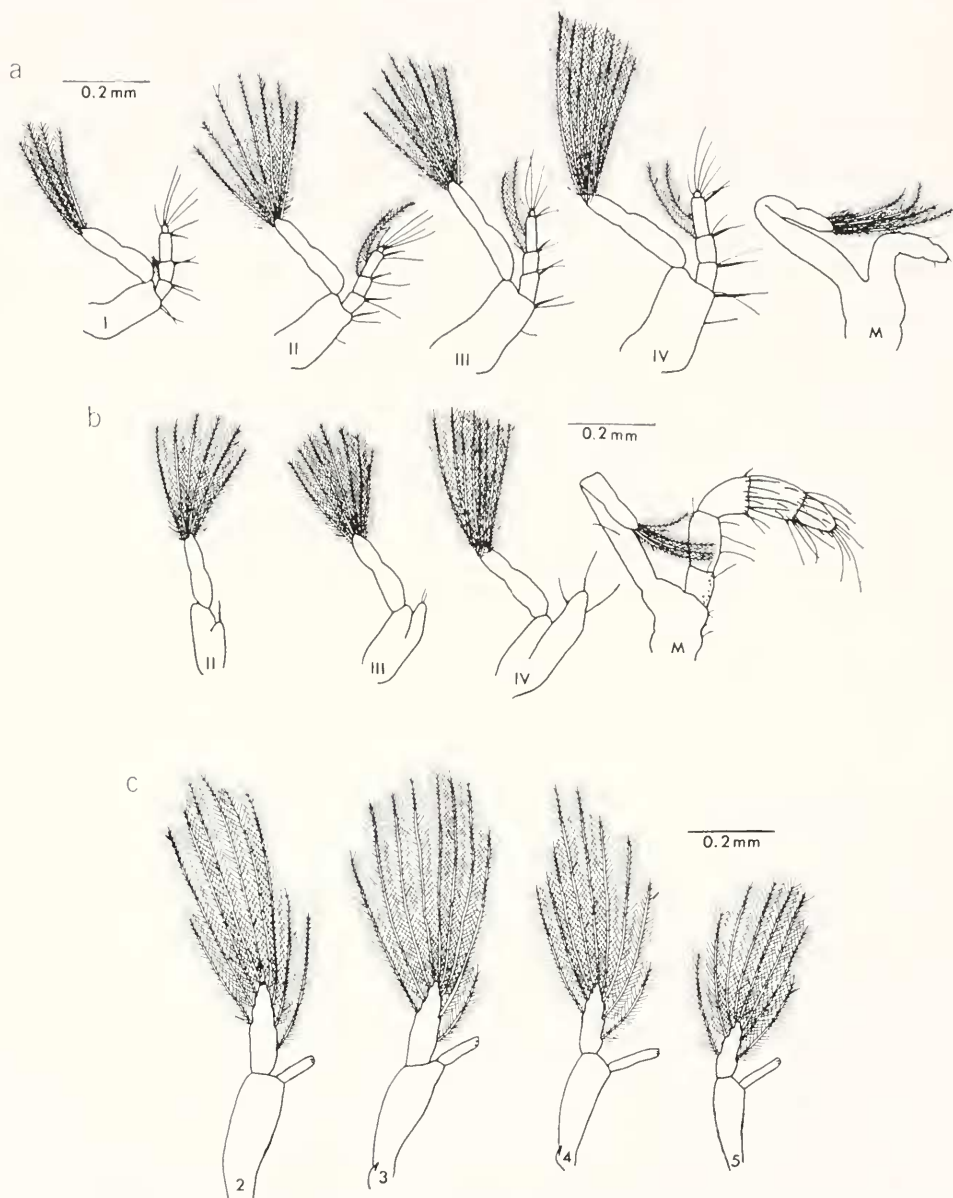


FIGURE 3. *Pagurus annulipes*; a. second maxillipeds of zoeal stages I-IV and megalopa, b. third maxillipeds of zoeal stages II-IV and megalopa, c. second through fifth pleopods of megalopa.

Zoea II

Duration 3.4 days ($N = 14$).

Carapace length 1.3-1.7 mm, av. 1.5 mm ($N = 40$).

Total length 2.3-3.1 mm, av. 2.9 ($N = 40$).

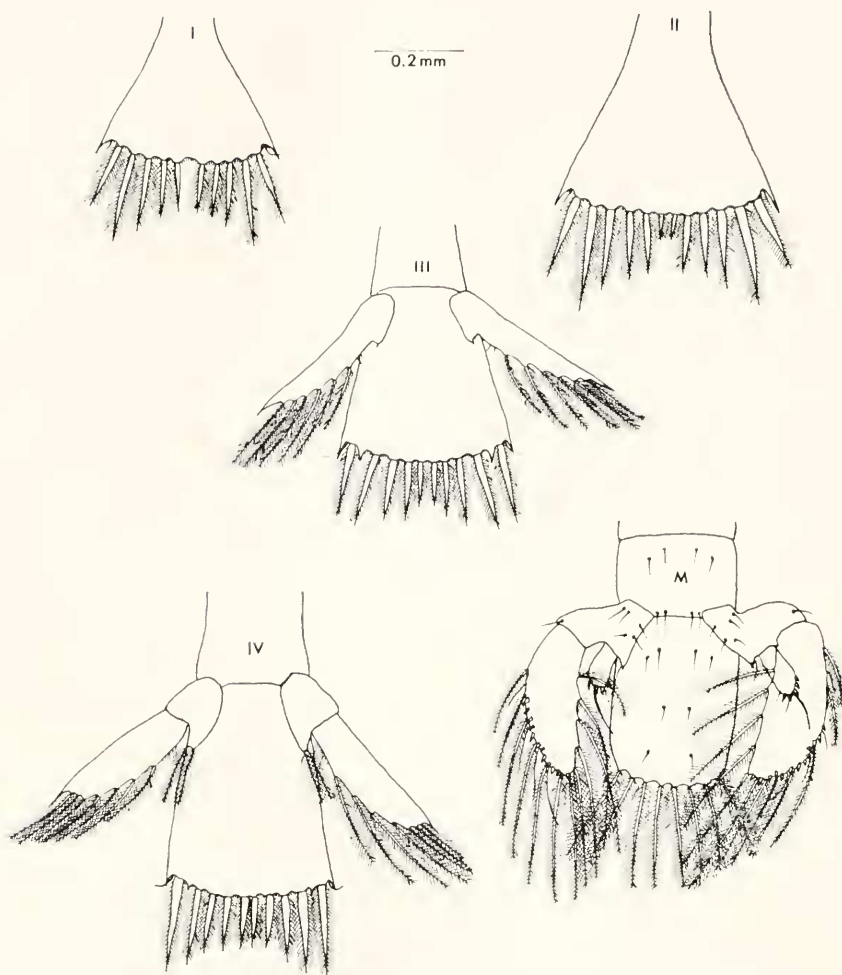


FIGURE 4. *Pagurus annulipes*; telsons of zoeal stages I-IV and megalopa, with uropods of zoeal stages III and IV and megalopa.

Mx 1—Basal endite with 4 strong spines, the 3 largest each bearing 2 or 3 cuneate spinules (similar in zoea III).

Mxp 3—Endopod bud with 1 or 2 terminal setae.

Zoea III

Duration 4.0 days ($N = 7$).

Carapace length 1.5–1.8 mm, av. 1.7 mm ($N = 10$).

Total length 2.8–3.2 mm, av. 3.0 mm ($N = 10$).

Sixth abdominal segment distinct, with uropods.

Pigmentation unchanged except for the appearance of small yellow chromatophores, 1 at the base of each eye and 1 medially in abdominal segment 2.

A 1—Outer ramus with 1 long and 2 or 3 shorter terminal aesthetascs plus 2 or 3 short setae. Distal end of peduncle with 1 to 3 small setae.

Zoea IV

Duration 2 days ($N = 1$).

Carapace length 1.9–2.1 mm ($N = 3$).

Total length 3.7–3.9 mm ($N = 3$).

Carapace, rostrum and abdomen segment number unchanged. Pleopod buds present.

Pigmentation unchanged except for the appearance of a yellow chromatophore at the base of each antennule.

A 1—Outer ramus with 1 long and 3 or 4 shorter terminal aesthetascs and 1 or 2 smaller setae also with 4 or 5 median aesthetascs. Distal end of peduncle with 2 or 3 small setae.

Mx 1—Coxal endite with 6 or 7 stout setae. Endopod with 2 or 3 terminal non-plumose setae.

Megalopa

Duration not determined.

Carapace length 1.3–1.7 mm ($N = 4$).

Total length 2.7–3.2 mm ($N = 4$).

Carapace nearly like adult. Posterolateral spines gone. Rostrum reduced and rounded. Eyes stalked with eye scales present. Abdomen with 6 segments, slightly asymmetric.

Pigmentation greatly elaborated. Of particular interest is incipient banding of the second and third pereopods, suggesting the adult pattern.

A 1—Outer ramus terminated with 1 long and 2 or 3 short setae. Inner ramus with 5 or 6 short terminal setae.

A 2—Flagellum of 10 to 14 segments.

Mx 2—Proximal lobe of coxal endite with 5 or 6 setae. Proximal lobe of basal endite with 7 to 10 setae, distal lobe with 7 to 11 terminal and 2 sub-terminal setae. Scaphognathite with 35 or 36 plumose setae.

Mxp 1—Coxal endite with 4 or 5 setae.

P 4—Subchelate, propodus with a single row of 5 to 7 tubercles representing adult rasp, dactylus with 1 to 3 tubercles.

Pl 2 to 4—Exopod with 8 long and 1 (2) short plumose seta.

U—Exopod with 12 or 13 plumose and 3 to 5 shorter non-plumose setae and with 11 to 13 tubercles. Endopod with 2 or 3 non-plumose setae and with 4 or 5 tubercles.

Pagurus pollicaris (see Figs. 5–10): *Zoea I*

Duration at room temperature 3.8 days ($N = 26$), at 16° C 11.6 ($N = 17$).

Carapace length 1.6 mm, total length 2.8 mm.

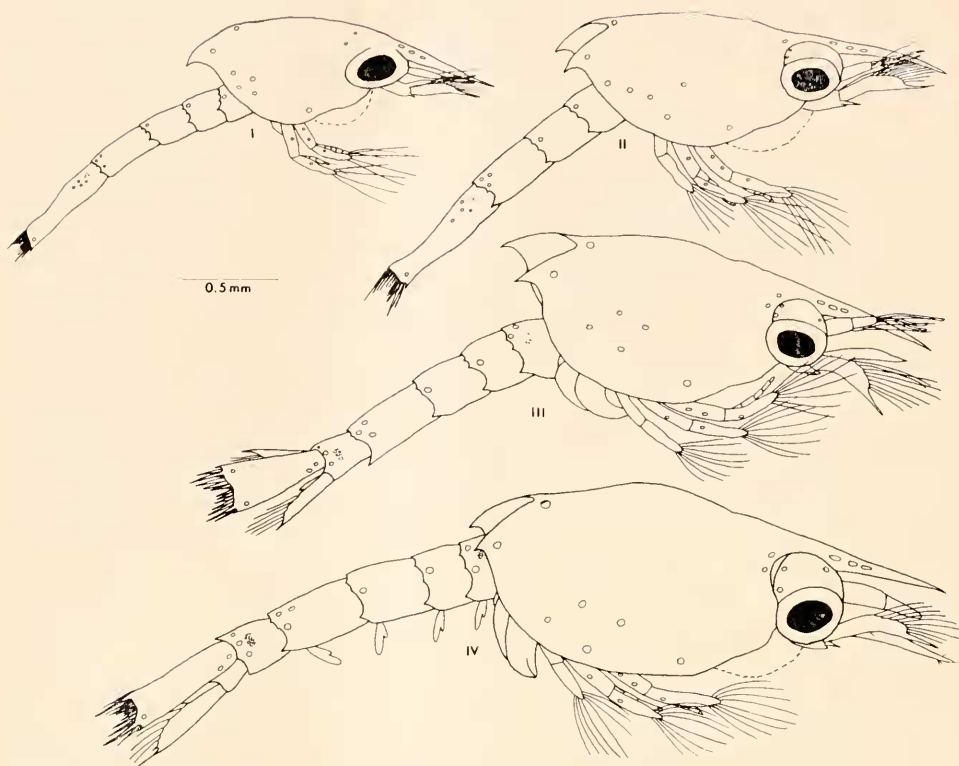


FIGURE 5. *Pagurus pollicaris*; zoeae I-IV, lateral view. Open circles represent yellow chromatophores; stippled, red.

Yellow chromatophores predominate. Three small yellow chromatophores on posterior half of rostrum. Red chromatophore complex from the base of the antennule posteriorly on each side of the labrum to the base of the mandibles. Yellow chromatophore towards base of each antennae. Two yellow chromatophores towards the outer margin of the bases and 1 towards the inner margin of the exopods of the first maxillipeds. One yellow chromatophore towards outer margin of the bases and 1 towards the inner margin of the exopods of the second maxillipeds. Carapace with 1 or 2 pairs of yellow chromatophores between the eyes, with single yellow chromatophore on midlateral edge of each side, with group of 4 to 6 yellow chromatophores towards posterolateral edge on each side, with 1 yellow chromatophore towards each posterolateral spine, and with a single yellow chromatophore at posteromedial edge. Abdominal segment 1 with 1 or 2 dorsal posteromedial yellow chromatophores, segment 2 with single or pair of posteromedial and a pair of posterolateral yellow chromatophores, segments 3 and 4 with pair of posterolateral yellow chromatophores, segment 5 with 3 pairs of posterolateral yellow chromatophores, segment 6-telson with pair of anteromedial red chromatophores followed posteriorly by 4 pairs of yellow

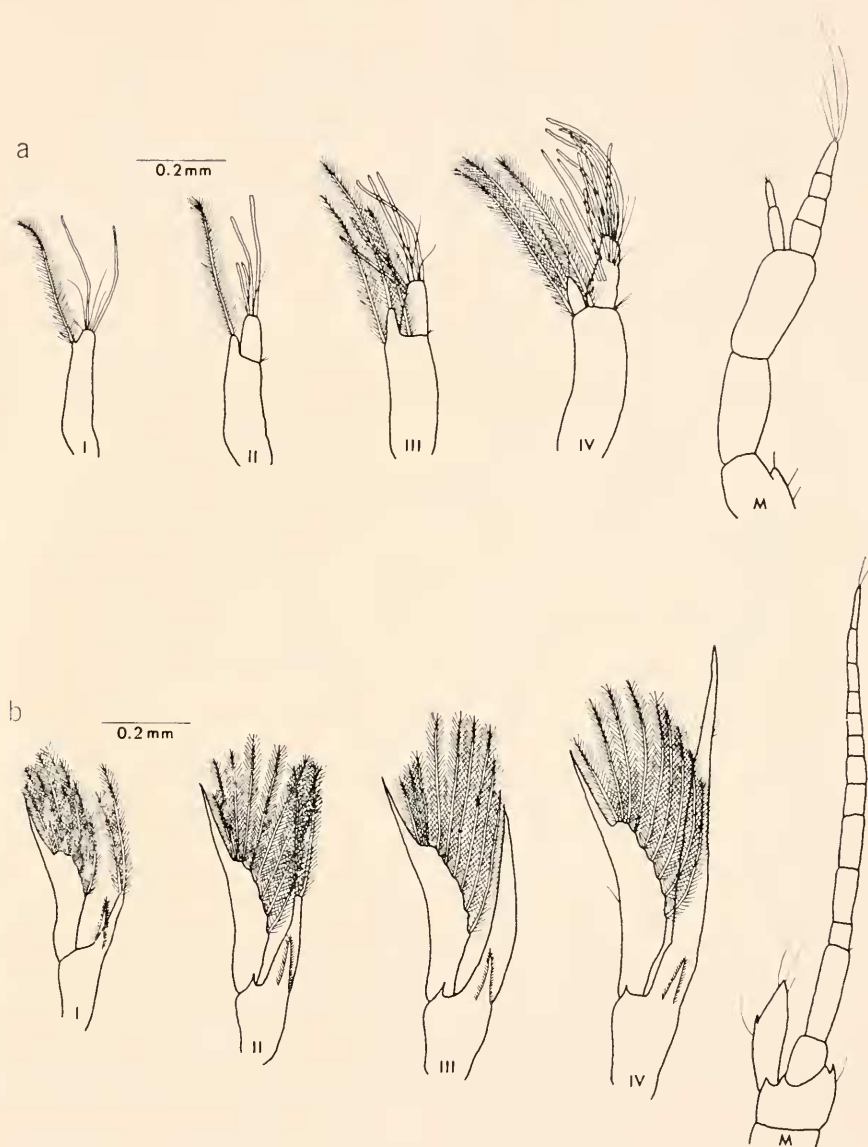


FIGURE 6. *Pagurus pollicaris*; a. antennules, b. antennae of zoeal stages I–IV and megalopa.

chromatophores plus a pair of posterolateral yellow chromatophores. Diffuse yellow pigment over dark pigment of eyes.

A 1—3 or 4 terminal setae.

Mx 1—Basal endite produced into 2 strong spines with 2 or 3 cuneate spinnules each.

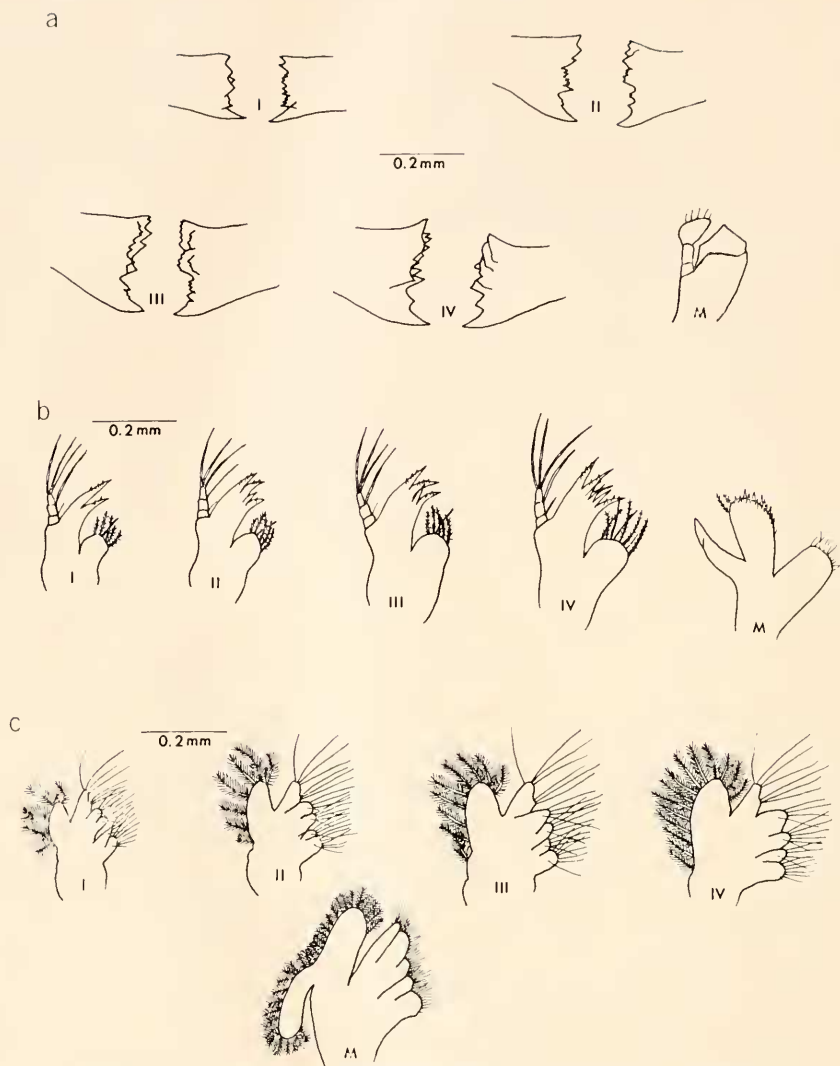


FIGURE 7. *Pagurus pollicaris*; a. mandibles, b. maxillules, c. maxillae of zoeal stages I-IV and megalopa.

Mxp 1—Basis with 6 long and 3 or 4 short medial setae (Mxp 1 similar in zoea II, III, IV). Endopod segment 1 with 3-4 setae.

Mxp 2—Basis with 2 or 3 short medial setae (similar in zoea II, III, IV). Endopod segment 1 with 1 stout and 1 or 2 finer setae.

Zoea II

Duration at room temperature 3.2 days ($N = 46$), at 16° C 10.8 ($N = 11$). Carapace length 1.8 mm, total length 3.2 mm.

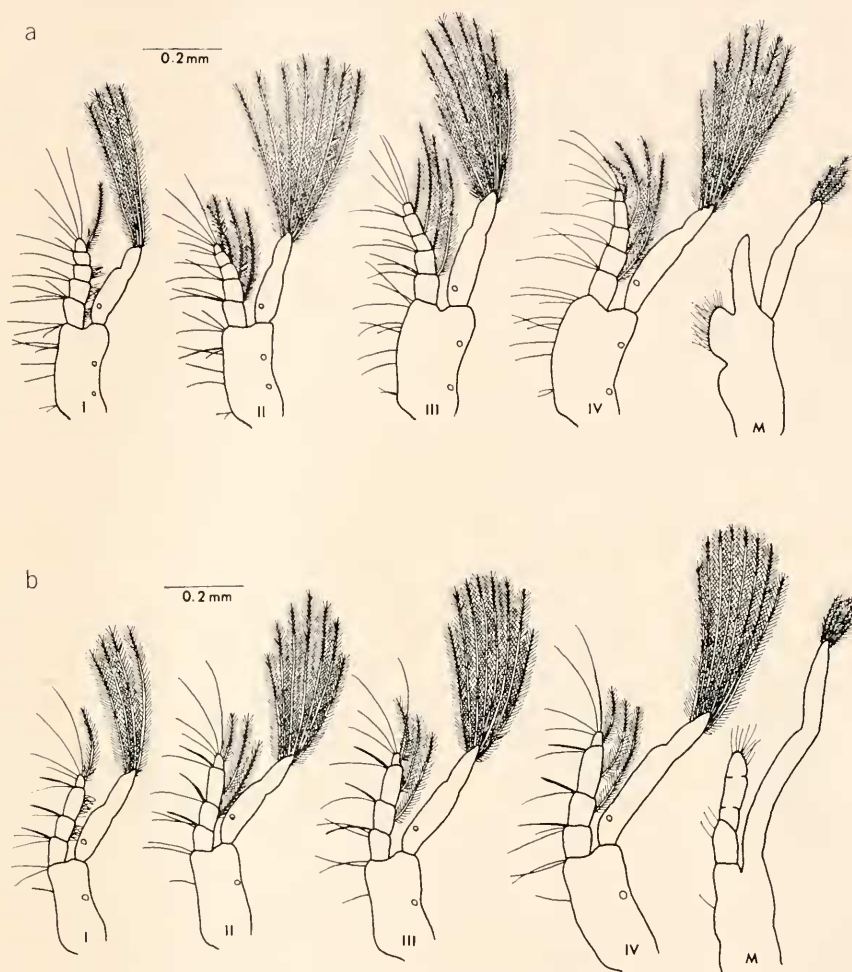


FIGURE 8. *Pagurus pollicaris*; a. first maxillipeds, b. second maxillipeds of zoeal stages I-IV and megalopa.

Pigmentation unchanged except for the addition of 1 or 2 posterior yellow chromatophores in each eye and of a median dorsal red bar-shaped chromatophore in abdominal segment 2.

A 1—Outer ramus with 2 or 3 short setae. Distal end of peduncle with 1 or 2 small setae on outer edge (similar in Zoea III).

Mx 1—Basal endite with 4 strong spines bearing 0 to 3 cuneate spinules (similar in Zoea III).

Zoea III

Duration at room temperature 3.6 days ($N = 33$), at 16° C 13.8 ($N = 9$).

Carapace length 2.1 mm; total length 3.5 mm.

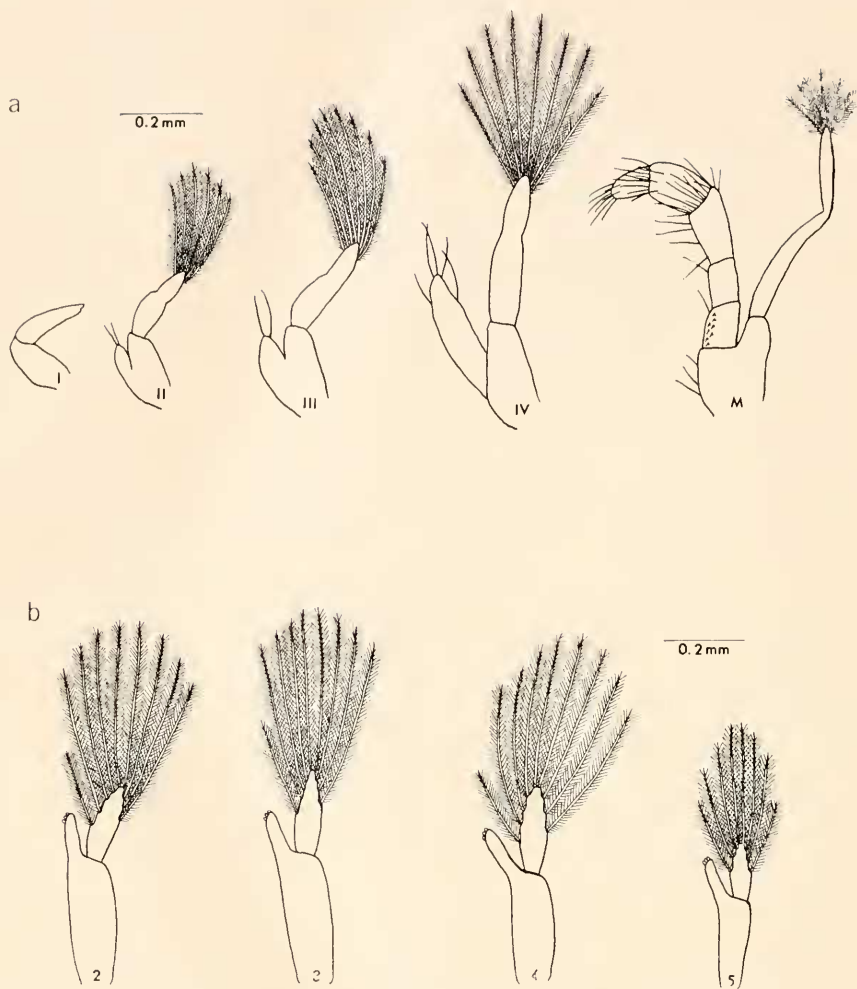


FIGURE 9. *Pagurus pollicaris*; a. third maxillipeds of zoeal stage I-IV and megalopa, b. second through fifth pleopods of megalopa.

Pigmentation unchanged except for the addition of 1 anterior yellow chromatophore in each eye.

A 1—Outer ramus with 3 or 4 setae.

Zoca IV

Duration at room temperature 4.6 days ($N = 15$), at 16°C 20.5 ($N = 2$).
Carapace length 2.2 mm, total length 3.8 mm.

Pigmentation unchanged.

A 1—Outer ramus with 3 incipient segments; segment 3 with 5-6 terminal aesthetascs. Distal end of peduncle with 2 or 3 small setae.

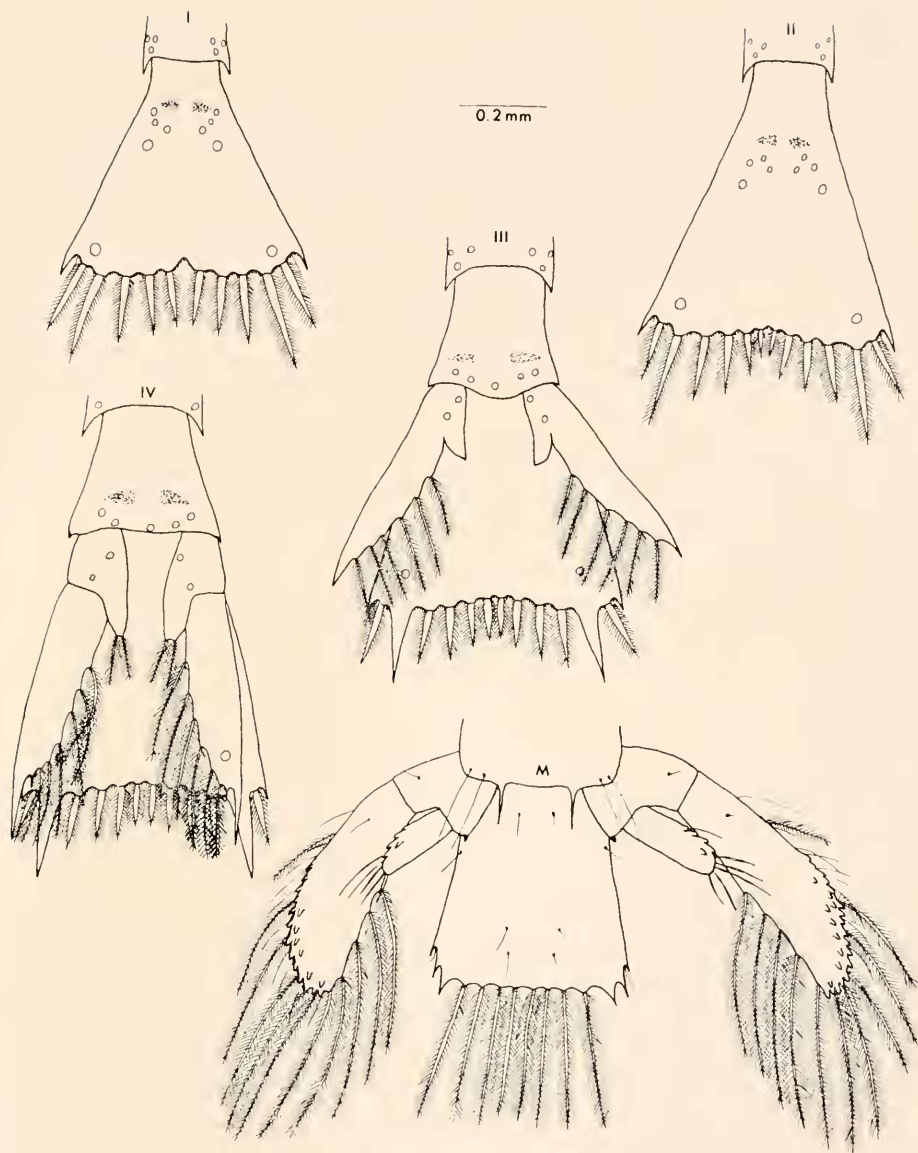


FIGURE 10. *Pagurus pollicaris*; telsons of zoeal stages I-IV and megalopa, with uropods of zoeal stages III and IV and megalopa.

Mx 1—Coxal endite with 7 or 8 stout setae.

Mx 2—Proximal lobe of basal endite with 5 or 6 terminal setae and 1 medial.

Megalopa

Duration, carapace and total lengths not determined.

Pigmentation not able to be determined, presumed to be predominantly yellow chromatophores. Aesthetasc number on A 1 not able to be determined.

A 2—Flagellum of 12 to 14 segments.

Mx 2—Proximal lobe of coxal endite with 8 to 10 terminal setae, distal lobe with 10 to 12. Proximal lobe of basal endite with 8 to 11 terminal setae, distal lobe with 8 to 12. Endopod unsegmented with 7 to 12 terminal setae.

Mxp 1—Exopod with 4 or 5 short plumose setae.

Mxp 2—Endopod with scattered short setae, 7 to 9 terminally. Exopod with 6 or 7 short terminal plumose setae.

Mxp 3—Exopod with 6 or 7 terminal plumose setae.

P 4—Subchelate, propodus with single row of 6 or 7 tubercles representing adult rasp, dactylus with 2 or 3 tubercles.

P 5—Propodus with tubercles in 4 rows totalling 14 to 16, dactylus with 3 or 4 tubercles and several short setae.

Pl 2 to 4—Exopod with 9(10) plumose setae.

U—Exopod with 10 or 11 long plumose setae and 8 to 12 shorter non-plumose setae, with 19 to 26 lateral and terminal tubercles. Endopod with 4 or 5 non-plumose setae, with 5 to 7 tubercles.

Larval key to three species of the genus Pagurus found in the Woods Hole, Massachusetts region

All species pass through 4 zoeal stages and 1 megalopa.

Key to Larval stages

1. Carapace without long rostrum, maxillipeds for feeding, 5 pairs of segmented functional pereopodsmegalopa
Carapace with long rostrum, maxillipeds with natatorial setae, pereopods unsegmented or weakly segmented rudiments2
(zoea)
2. Uropods present3
Uropods absent4
3. Uropod with exopod free from basisfourth zoea
Uropod unsegmentedthird zoea
4. Telson with 12 articulated plumose setae, third maxilliped functional with natatorial setaesecond zoea
Telson with 10 articulated plumose setae, third maxilliped rudimentary without setaefirst zoea

Key to Species

For living or freshly killed larvae.

Zoeae and Megalopae

1. Few scattered mostly red chromatophores*P. longicarpus*
Numerous chromatophores2
2. Red chromatophores predominate: very large red chromatophore on each mid-lateral portion of carapace and large red chromatophore in abdominal segments 2-3, megalopal pereopods 2 and 3 with incipient red banding*P. annulipes*

Yellow chromatophores predominate: many on carapace at least 1 pair per abdominal segment, and one on posterolateral sides of telson*P. pollicaris*

For preserved larvae.

Zoeae

1. Ventrolateral spines of abdominal somite 5 long, almost reaching telson*P. longicarpus*
 Ventrolateral spines of abdominal somite 5 medium, not much larger than those of other somites2
2. Maxillulary endopod with 3 terminal setae, telson process 4 of zoea III and IV longest*P. pollicaris*
 Maxillulary endopod with 2 terminal setae, telson process 4 of zoea III and IV very small*P. annulipes*

Megalopae

Telson formula 4 + 4: all processes long articulated plumose setae*P. annulipes*
 Telson formula 5 + 5: process 1 minute spine, processes 2 to 5 long articulated plumose setae*P. longicarpus*
 Telson formula 8 + 8: processes 1, 3, and 4 small spines, process 2 a fine hair, and processes 5 to 8 long articulated plumose setae*P. pollicaris*

DISCUSSION

In 1903 Thompson illustrated from plankton material the larval stages of what he considered to be *Pagurus longicarpus*, although he was aware of a possible confusion with *P. annulipes*. In comparing the preceding description of *P. annulipes* with Thompson's figures, the following differences are noted: third zoea slightly smaller than Thompson's; antennal scale setation of zoea I to IV 8 long and 1 to 2 short, 9 long and 1 short, 10 long, 10 long in this study compared with 9 long and 1 short for all four zoeal stages in Thompson's; maxillulary basal endite of zoea II with 4 spines compared with 3 spines in Thompson's; maxillary scaphognathite setation of zoea II and III 7 and 9 compared with 6 and 10 in Thompson's; first and second maxilliped exopod setation of zoea II 7 compared with 6 in Thompson's; megalopal pleopod 2 to 5 setation 9 (10), 9 (10), 9 (10), 8 compared with 7, 7, 9, 7 in Thompson's. These differences are minor when compared with the overwhelming similarity between his figures and this description. It is clear that Thompson in reality figured the larval stages of *P. annulipes*, not *P. longicarpus* (see Roberts, 1970). Although Thompson states that larvae of both species are found in plankton samples taken in Woods Hole during the summer, confusion arose from his assumption that, since the adults of *P. longicarpus* are considerably larger than those of *P. annulipes*, the larvae of *P. longicarpus* likewise would be larger. Just the opposite is the case; *P. annulipes* larvae are the larger.

Roberts (1970) has made a detailed comparison of *P. annulipes* and *P. longicarpus* in his Table II. In addition to the differences which he noted are the following: *P. annulipes* zoeae have a large bar-shaped yellow chromatophore in

the cardiac region of the thorax, *P. annulipes* maxilliped exopod setation of zoea III is 7 compared with 8 in *P. longicarpus*, the uropod exopod of *P. annulipes* zoea IV has 1 terminal spur compared with 1 or 2 in *P. longicarpus*, and the megalopa of *P. annulipes* does not have a minute lateral spine on each side of the telson.

MacDonald, Pike and Williamson (1957) divide *Pagurus* larvae into two groups, A and B, separated by 9 zoeal and megalopal characteristics (see Roberts, 1970, Table III). Pike and Williamson (1960) propose a third group C, which shares 2 of the 9 characteristics with group A larvae, 5 with group B, and which has 3 similar to neither group. Roberts (1970) proposes a fourth group D for *P. longicarpus*, which shares 3 of the 9 characteristics with group A larvae, 4 with B, and in 2 is not similar to group A, B or C. *P. annulipes* larvae differ from those of group B in 3 respects: possessing a yellow chromatophore over the stomach region as in group A, having medium length lateral spines on abdominal segment 5 as in group C and having a megalopa with antennae about equal in length to the major cheliped as in group D. From the preceding description of *P. pollicaris* larvae it is seen that they differ from group B also in 3 respects: having telson process 4 of zoea III and IV long and fused with the telson as in group A, possessing medium length lateral spines on abdominal somite 5 as in group C and having a unique antennal scale setation.

Several points need to be made pertaining to the validity and value of present grouping within the genus *Pagurus*. Characteristics used to distinguish the groups A, B, C and D are those observable without complete dissection of the larval appendages. Although not useful for quick identification, less easily observable characteristics of the appendages may be of equal or greater taxonomic significance. Another point is that complete larval descriptions for only 8 and partial descriptions for 9 *Pagurus* species have been reported (John C. Markham, School of Marine and Atmospheric Sciences, University of Florida, personal communication), out of more than 180 described species (Gordon, 1956). The 3 species most recently described would indicate the necessity of erecting a new group for each or of concluding that the presently proposed groups are neither taxonomically meaningful nor useful in facilitating plankton identification. The latter view is held here.

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SUMMARY

1. The external anatomy of 4 zoeal stages and a megalopa of *Pagurus annulipes* and *P. pollicaris* is described from laboratory-reared specimens.

2. Keys to the shallow-water hermit crab larvae of the Woods Hole, Massachusetts region are given, based on larval pigmentation and on external anatomy.

3. Comparison with Thompson's (1903) figures shows that he illustrated *P. annulipes*, not *P. longicarpus*.

4. Comparisons with other larvae of the genus *Pagurus* are made in context of an examination of currently proposed groups within the genus. The validity and usefulness of these groups is seriously questioned.

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